Three Pacific Species of "Lar" (Including a New Species), Their Hosts, Medusae, and Relationships. (Coelenterata, Hydrozoa)[1]

CADET HAND[2]

THE HYDROID "LAR," which lives as a commensal upon the tubes of sabellid polychaetes, has been described from the Atlantic by Gosse (1857) and from the Pacific by Uchida and Okuda (1941) and by Hand and Hendrickson (1950). Hincks (1872) noted that the medusae produced by *Lar sabellarum* Gosse were similar to *Willia stellata* Forbes, and later Browne (1896) clearly established that the medusa of *Lar sabellarum* was *Willia stellata*. Uchida and Okuda (1941), in their study of the Japanese "Lar," showed that their hydroid was that of the medusa *Proboscidactyla flavicirrata* Brandt and, as a result of their study together with the data of Browne and Kramp (1939), united the genera *Willia* and *Proboscidactyla*, retaining the name *Proboscidactyla* because of priority. Hand and Hendrickson (1950) described a new "Lar," *Proboscidactyla* sp., from California and suggested it might be the hydroid of the medusa *Proboscidactyla occidentalis* (Fewkes). Since 1950 the author has had an opportunity to examine medusae of *Proboscidactyla* from off the coast of Oregon, Monterey Bay, near Santa Cruz Island, and the San Diego region, the latter three localities all being in California waters. It also has been possible to obtain specimens of "Lar" from Puget Sound (Washington) and La Jolla, California. An examination of the hydroids and medusae has shown that three separate species of *Proboscidactyla* occur on the Pacific coast of the United States, a northern species (*P. flavicirrata*), a central species (*Proboscidactyla* sp. of Hand and Hendrickson 1950, named for the first time in the present report), and a southern species, *P. occidentalis*.

The definition of species in the Hydrozoa, more especially among the gymnoblasts, has long been based on rather gross, frequently ephemeral, characters such as size, shape, number and type of tentacles, arrangement of hydrorhizae, and the kinds of individuals present in the colony. In the following report, a not completely proved hypothesis has been used as one of the primary criteria of what is to be taken as a species. This concerns the nematocysts, and, briefly stated, the hypothesis is that each species of coelenterate can be identified by its possession of a unique group of nematocysts (the cnidom), at least with regard to size and shape, although not necessarily with regard to kind. This hypothesis has stemmed from the work of Weill (1934) and has proved acceptable for sea anemones as demonstrated by the numerous studies of Dr. Carlgren of Lund, Sweden. The work of E. G. Papenfuss (1936) on scyphomedusae and of F. S. Russell (1938) on hydromedusae lends much validity to the contention. To date no refutation of this hypothesis has been presented, and the study of the species of "Lar" demonstrates the further usefulness of nematocysts in the identification of hydroids. The terminology of nematocysts used herein is that of Weill (1934).

It will be noted in the following pages that the nematocysts of the hydroid stages are very similar from species to species. This, perhaps, is not unexpected as hydroids are immature

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organisms and would be expected to resemble one another more closely than the adults of different species. However, when we add the small differences in size and shape of nematocysts to the morphological differences of the hydroid stages, we find that these animals can be readily identified as separate species. The nematocysts of the medusae of these species, on the other hand, show greater differences, and again we would expect this, from the thesis that adults of related animals are less alike than their younger stages. It is, however, somewhat disappointing to discover that the medusoid and hydroid stages of a genus do not possess the same cnidom. Thus, in *Proboscidactyla* we find that the hydroids may be characterized as possessing a cnidom of three types of nematocysts (macrobasic euryteles, microbasic euryteles, and desmonemes), whereas the medusan cnidom consists of but two types (macrobasic euryteles and desmonemes). This should serve as a warning that hydroids and their medusae may not be identifiable with one another on a basis of their nematocysts. Moreover, this divergence of cnidoms in the two phases of the life history seems to imply that the nematocysts are adaptive characters which respond to environmental demands, and perhaps we should advance with caution along the road of relating larger groups such as genera and families on a basis of their nematocysts.

In the following discussion, in order to speak clearly of the arrangement of the tentacles and canals of the medusae of *Proboscidactyla*, a convention has been adopted in which the first four tentacles to develop are called *first order tentacles* and their canals are the *first order canals*. The second four tentacles arise to the right of the first order tentacles and are called *second order tentacles*. These tentacles arise at the margin of the bell at the point at which the *second order canals* join the ring canal. The *third order tentacles* are the the next eight tentacles which arise at the ends of the branches from the first and second order canals. Beyond the third order the arrangement of tentacles and canals is more difficult to discern. On specimens with 32 tentacles a rather clear *fourth order* of tentacles and canals can usually be made out, but on specimens with more than 32 tentacles the arrangement seems to have lost the regularity presented by the younger medusae. It has been noticed that, after the first order canal gives rise to the second order branch on its right and the third order branch on its left, it usually does not branch again and that most later branches arise from either the second and third order canals or from the rather diffuse fourth order.

The following material, upon which part of the descriptions presented herein are based, has been deposited in the U. S. National Museum.

1. *Proboscidactyla flavicirrata*, adult medusae, 20 specimens, U.S.N.M. 50035.
2. *P. flavicirrata*, hydroids on tubes of *Schizobranchia* and *Pseudopotamilla*, 6 specimens, U.S.N.M. 50036.
3. *P. flavicirrata*, hydroid on *Schizobranchia*, 1 specimen, U.S.N.M. 50037.
4. *Proboscidactyla circumsabella*, HOLOTYPE, adult medusa, 1 specimen, U.S.N.M. 50038.
5. *P. circumsabella*, paratypes, medusae, 8 specimens, U.S.N.M. 50039.
6. *P. circumsabella*, hydroids on *Pseudopotamilla*, 11 specimens, U.S.N.M. 50040.
7. *Proboscidactyla occidentalis*, medusae, 12 specimens, U.S.N.M. 50041.
8. *P. occidentalis*, hydroid on *Pseudopotamilla*, 1 specimen, U.S.N.M. 50042.

Proboscidactyla flavicirrata Brandt

THE MEDUSA: This medusa was first described by Brandt (1834) from the north Pacific and has subsequently been found near Japan and as far south as Puget Sound on the American side of the Pacific. Twenty-eight specimens of this medusa taken during August, 1949, have been found in plankton samples collected in the area from the mouth of the Columbia River on the north to Cape

Blanco, Oregon, on the south and at a distance of from 40 to 200 miles from shore. This plankton was collected by the Scripps Institution of Oceanography as part of its work on the California Cooperative Sardine Research Program. All the specimens observed possessed four first order radial canals and were in adult or nearly adult condition. The diameter of the bell varied from 6 to 10 millimeters and the height from 6 to 8 millimeters. They possessed from 40 to 72 tentacles.

The branching of the radial canals is very complex and highly irregular although the number of terminal branches in each quadrant is nearly equal on any given specimen. Thus, on a specimen possessing 72 tentacles, the quadrants had 17, 18, 18, and 19 tentacles,

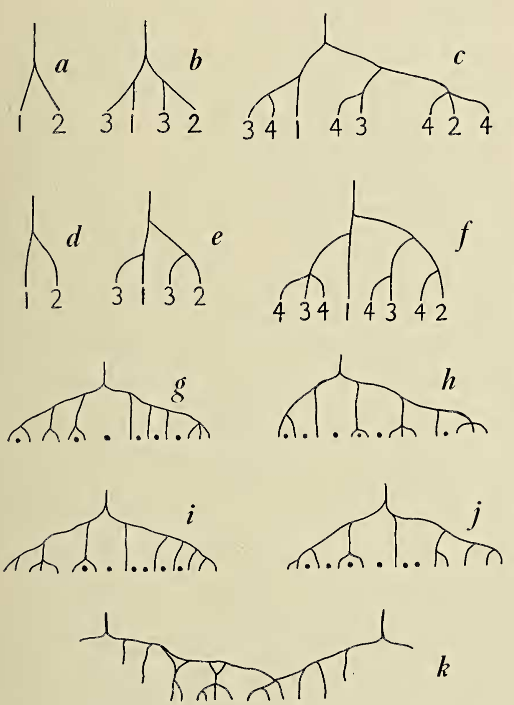

FIG. 1. *a–c, Proboscidactyla occidentalis; d–f, P. circumsabella:* and *g–k, P. flavicirrata,* showing (diagrammatically) the branching of the radial canals. The numbers in figures *a* to *f* refer to the order of the canals and tentacles. The spots between the ends of the canal branches in figures *g* to *j* represent the position of tentacles to which no canals could be seen to be branching.

respectively. This condition is illustrated by Figure 1*g–j*. It will be noted that a canal branch does not run to each tentacle. In most specimens it appeared that the tentacles were more numerous than the canals, which condition may or may not actually exist, as the specimens examined were badly contracted and it was difficult to determine the distribution of the radial canals. In one specimen an anomalous condition was found in which the canals from two adjacent quadrants had anastomosed (Fig. 1*k*).

Cnidothylacies (nematocyst sacs) are present on the exumbrellar surface and are connected to the solid ring canal by a chord of what are presumed to be endodermal cells. In many specimens no ring canal can be found, and here the chord of cells merely ends where the canal used to be. Uchida and Okuda (1941) noted that the ring canal of this species degenerates as the medusa matures, whereas Browne (1906) suggested that the disappearance of the ring canal was not unexpected, as each tentacle is directly connected to the stomach via the system of branched canals. The cnidothylacies never occur in association with the first order tentacles but can be found above all other tentacles and in the intertentacular spaces. Most specimens, however, show a somewhat irregular distribution of these structures, and the greatest number observed in any one quadrant was 14.

When this medusa is adult the gonads appear as white to creamy (formalin-preserved color) folded masses covering most of the stomach. The four gonadial masses present occupy interradial positions, each mass being developed as a pair of thickened lobes upon the adradial sides of the quadratic stomach with a thin sheet of gonadial tissue connecting the two lobes and covering the stomach wall. The gonads do not appear to fuse across the radial margins of the stomach. The lips of the manubrium are highly folded and hang but a short distance below the oral end of the gonads. Figure 2 illustrates the several features just mentioned.

The tentacles, which are inserted into the bell margin by endodermal bulbs, were quite contracted in most specimens; however, it was immediately apparent that the older tentacles are somewhat longer and larger than the younger ones. The tentacle bulbs are light yellow to cream in color and much more opaque than the tentacles.

The shape and general appearance of the medusa is shown in Figure 2, although only one quadrant is shown with all its details. It will be noted that there are four interradial, subumbrellar pouches which extend the subumbrellar cavity well above the level of the stomach. This is a characteristic of all three of the species described in this paper.

The nematocysts of the genus *Proboscidactyla* are known for the hydroid in two instances (Russell, 1938; Hand and Hendrickson, 1950) and in one case for the medusa (Hand and Hendrickson, 1950) and in this latter case only for very immature medusae. The nematocysts of adult *P. flavicirrata* were studied, and a simple cnidom of two types was found as follows:

Cnidothylacies
- Macrobasic euryteles . . . 22—30×9—14μ
- Desmonemes . . . . 5— 7×4— 6μ

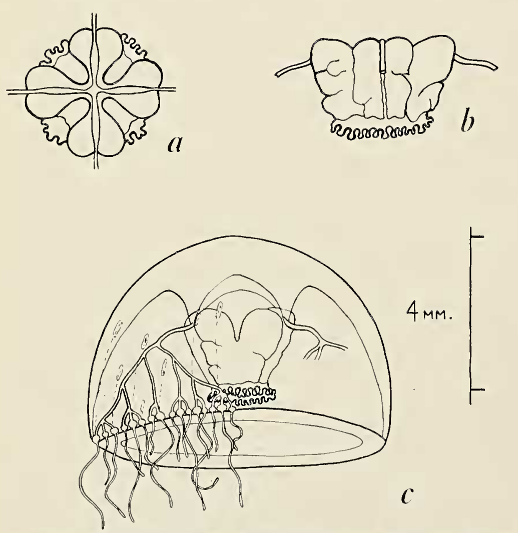

FIG. 2. *Proboscidactyla flavicirrata. a*, Aboral view of the stomach; *b*, side view of stomach; *c*, whole medusa with only one quadrant shown in detail.

Tentacles
- Macrobasic euryteles . . . 8—12×5— 7μ
- Desmonemes . . . . 5— 7×4— 6μ

Figure 3*a–c* illustrates the nematocysts. The desmoneme of the cnidothylacies appears to be identical to that of the tentacles.

THE HYDROID: Uchida and Okuda (1941) have given a rather complete description of this hydroid, although a few additional remarks and comparisons of their report with material from Puget Sound seems desirable. Several colonies of this hydroid were collected during the summer of 1950 in Puget Sound by Dr. Ralph I. Smith of the University of California at Berkeley and were given to the author for study. Detailed notes and sketches of the appearance and color of this hydroid in life were also gratefully received from Dr. Smith.

The organization and arrangement of individuals in *P. flavicirrata* are quite different from those of the other Pacific species. The gastrozooids and gonozooids stand in a double row or ring around the lips of sabellid tubes with the gastrozooids innermost, while the naked hydrorhizae tend to form parallel rows extending several millimeters along the long axis of the worm tube with occasional random anastomoses. The gonophores may arise either from the hydrorhiza near the base of an adjacent gastrozooid or actually from the proximal portion of the gastrozooid (Fig. 4*b*, *c*). What are presumed to be young or abortive gonozooids may occasionally be found at almost any point among the hydrorhizae, although they were not as numerous as those found by Uchida and Okuda. Where young or new gonozooids are forming on the bases of the gastrozooids, the appearance is that the gastrozooid is growing a tail (Fig. 4*a*). Figure 4*b* illustrates the general appearance and organization of a colony.

A total of 16 colonies was observed, and of these seven showed strongly parallel hydrorhizal nets and the remaining nine varied from a reasonably close approach to parallel

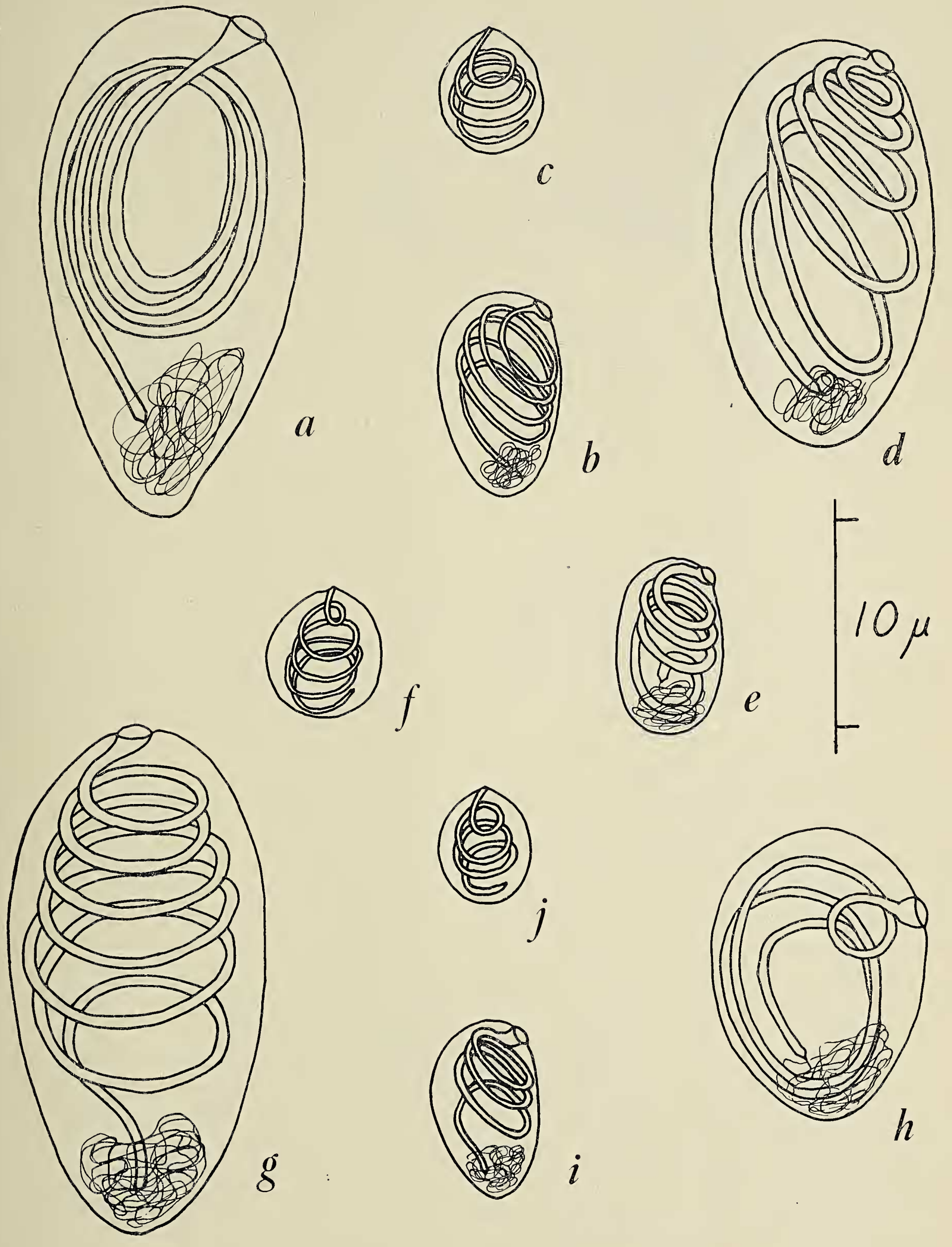

FIG. 3. The nematocysts of the medusae. *a–c, Proboscidactyla flavicirrata; d–f, P. circumsabella; g–j, P. occidentalis. a, b, d, e, g, h, i* are macrobasic euryteles; *c, f, j* are desmonemes.

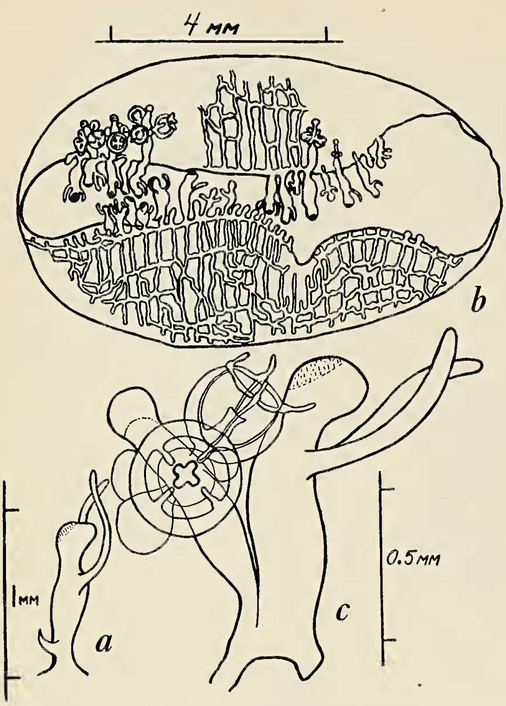

FIG. 4. The hydroid of *Proboscidactyla flavicirrata*. *a*, Young gastrozooid with a "tail"; *b*, a colony, only part of which is shown, as seen by looking down upon the end of a worm tube; *c*, gastrozooid and gonozooid, the latter with several medusa buds.

networks to very random, irregular networks. It was noted that the nine colonies showing the less parallel hydrorhizal networks also possessed very slightly smaller gastrozooids than the other seven colonies and that these nine colonies were the only ones possessing scattered gonozooids or no gonozooids at all. Some of these colonies were obviously immature, whereas others were quite mature. It was thought that these nine colonies might be of some other species, but this idea was discarded as no differences between these and the larger colonies could be found in their nematocysts. So far no one has demonstrated whether a single colony of "Lar" produces only one sex of medusa or whether both sexes can be produced by a single colony, so the suggestion may be tentatively put forth that the visible morphological differences in the Puget Sound "Lar" may be of a sexual nature.

The color of this hydroid in life is, in general, orange to pink with the color restricted to the endoderm as in other species. The gastrozooids are 0.8–1.2 millimeters tall by about 0.2 millimeter in diameter. The gonozooids are in general thinner and slightly shorter than the gastrozooids. Two tentacles are present on the gastrozooid and none on the gonozooid. The size of the Puget Sound individuals is slightly larger than that of those from Japan, and no variation in tentacle number was noted, whereas a number of specimens with extra tentacles was reported from Japan. The Puget Sound "Lar" possessed from two to eight medusa buds, commonly eight, with four of the buds large and well developed and four as small, poorly developed medusae. The four small buds alternate with the four large ones, and all buds seem to arise at a single level slightly above the middle of the gonozooid.

The nematocysts of the hydroid are as follows:

Macrobasic euryteles.....	$17-25 \times 8-12\mu$
Large microbasic euryteles	$10-18 \times 4-6\mu$
Small microbasic euryteles	$5-6 \times 2-3\mu$
Desmonemes...........	$3-5 \times 2-4\mu$

The tentacles of the polyps seem to possess only the small microbasic euryteles listed above, whereas the three remaining types were found in the caps of the polyps. The desmoneme and the large microbasic eurytele also occur in small numbers over the surfaces of the polyps. Figure 5*a–d* illustrates the appearance of the nematocysts of this hydroid.

THE HOSTS: Uchida and Okuda (1941) reported this species upon the sabellid, *Potamilla myriops.* Berkeley and Berkeley (1952) do not list this species for the Puget Sound area but do list *Potamilla neglecta*, which is one of the hosts for *Proboscidactyla occidentalis*, the third species of this report. *Proboscidactyla flavicirrata* occurred on two species of sabellids in the Puget Sound area, namely *Schizobranchia insignis* and *Pseudopotamilla ocellata.* Ten genera of sabellids were reported by

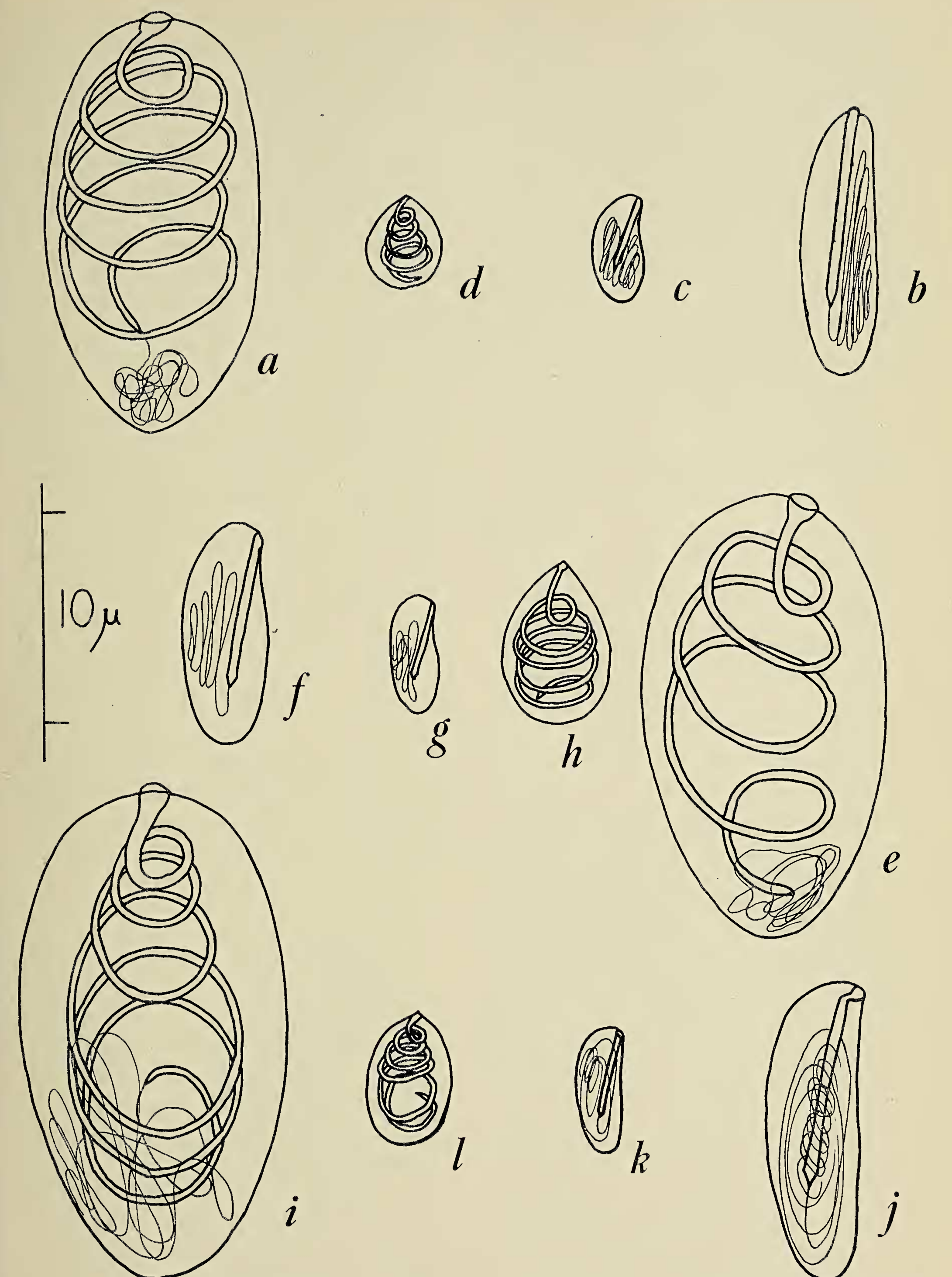

FIG. 5. The nematocysts of the hydroids. *a–d*, *Proboscidactyla flavicirrata; e–h, P. circumsabella; i–l, P. occidentalis.* *a*, *e*, *i* are macrobasic euryteles; *b*, *c*, *f*, *g*, *j*, *k* are microbasic euryteles; *d*, *h*, *l* are desmonemes.

Berkeley and Berkeley (1952) from the Pacific area around Puget Sound, with a total of 19 species involved. It seems likely that further observation will reveal the presence of this hydroid upon still more sabellids than the three from which it has been reported to date.

The observed difference in size of individuals and in colony morphology reported in the description of this hydroid does not seem to be correlated with the host upon which the colony is growing. Colonies with both parallel and irregular hydrorhizal nets were found upon both of the sabellids reported above as hosts for *Proboscidactyla flavicirrata* in the Puget Sound area.

Proboscidactyla circumsabella sp. nov.

The hydroid and young medusa of this species were first described by Hand and Hendrickson (1950) under the name of *Proboscidactyla* sp. Since that description appeared, a series of medusae of this species ranging from small immature specimens to adults have been obtained from plankton from Monterey Bay. I am indebted to Mr. Frank Gwilliam and Mr. Meridith Jones of the University of California at Berkeley for some of these specimens.

As the hydroid and young medusa have already been described, it does not seem necessary to repeat the whole diagnosis at this time, but certain salient features are worth repeating for the sake of comparison with the other two species considered here.

THE MEDUSA: Adult medusae were collected during the months of June and July, 1951, and a single specimen during July, 1952. A total of nine adult medusae have been examined.

The largest specimen observed measured 3.0 millimeters, bell diameter, by 2.5 millimeters high. This specimen possessed 32 tentacles and 28 cnidothylacies. The gonads were well developed and occurred in the interradial position as four paired masses of simple swollen lobes on the adradial sides of the stomach. Figure 6*a–c* illustrates the appearance of a living, 24-tentacled, adult medusa as well as the details of the shape and location of the gonads and the lips of the manubrium. The manner in which the lips fold seems to be characteristic of this species.

From a study of the nine medusae in hand, it appears that a rather regular system of branching of the radial canals obtains in this species, with the result that the adult medusae are quite uniform. Of the specimens examined only a single one deviated from the pattern of development presented in Figure 1*d–f*. This single specimen possessed 25 tentacles, the single unusually located tentacle occurring to the right of the second order tentacle of one quadrant and connected to the second order canal by a short canal of its own. In immature or developing medusae there is an obvious difference in tentacle length, tentacle bulb diameter, and radial canal size; the older tentacles, tentacle bulbs, and radial canals are longer or larger, and thus the developing complexity of the canal system is readily visible. From the time the medusae reach the 16-tentacle stage until they attain the 32-tentacle condition the exact order of appearance is not precise; therefore, specimens may have odd numbers of tentacles, although the end result is uniform as judged by the four specimens which possessed 32 tentacles.

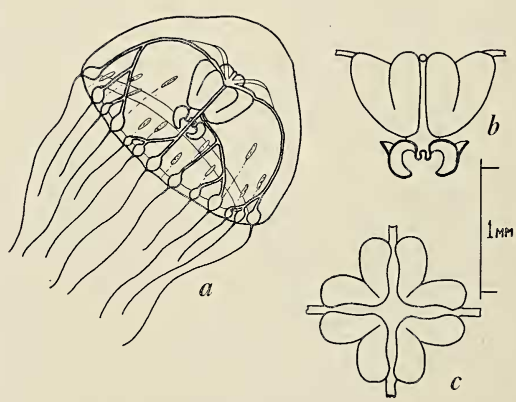

FIG. 6. *Proboscidactyla circumsabella*. *a*, Whole medusa, with tentacles shown on one half only; *b*, side view of stomach; *c*, aboral view of stomach.

In life this medusa is nearly colorless, pigment being restricted to the tentacle bulbs and the wall of the stomach. These areas are brown to orange brown. The tentacle bulbs appear to develop before pigment is deposited in them so that the small tentacle bulbs are colorless or nearly so. The older tentacle bulbs are usually a bright orange-brown color. The gonads are very lightly colored, those of the males being white and of the females a light creamy color. The sexes are separate.

The nematocysts of adult *P. circumsabella* are as follows:

Large macrobasic euryteles	17—26×8—12μ
Small macrobasic euryteles	7—10×4— 5μ
Desmonemes	5— 7×4— 6μ

The large macrobasic euryteles are restricted to the cnidothylacies, whereas the small macrobasic euryteles occur in the tentacles. The desmonemes are present in both the tentacles and cnidothylacies. The large macrobasic euryteles occur in very small numbers, and not all cnidothylacies were found to possess them (Fig. 3*d–f*).

THE HYDROID: The hydroid is similar to other species of *Proboscidactyla* in that the colony possesses two major types of individuals, the two-tentacled gastrozooids and the gonozooids, which are without tentacles and bear the medusa buds. Small gonozooids or dactylozooids occur at the margins of the hydrorhizal network. The gonozooids occur as scattered individuals arising from the hydrorhizae and are never arranged in a row immediately behind or on the gastrozooids, as in *P. flavicirrata* or *P. stellata*. Up to a maximum of four medusa buds may be borne upon a single gonozooid. The individuals of a colony seldom are as much as 1 millimeter tall and are commonly about 0.8 millimeter tall by about 0.1 millimeter in diameter. The hydrorhizal network is devoid of any covering and may form extensive anastomosing nets running along the tube for as much as 15 millimeters.

The nematocysts of the hydroid are as follows:

Macrobasic euryteles	16—24×9—12μ
Large microbasic euryteles	9—12×3— 4μ
Small microbasic euryteles	5— 6×2— 3μ
Desmonemes	6— 8×3— 4μ

The macrobasic euryteles occur only in the cap of the gastrozooid and the tip of the gonozooid. The other three types of nematocysts occur in most areas of the gastrozooid and gonozooid although no small microbasic euryteles were found in the gonozooids. Figure 5*e–h* illustrates the nematocysts of the hydroid.

THE HOSTS: *Proboscidactyla circumsabella* occurs most commonly on the sabellid *Pseudopotamilla ocellata*. Careful observation of other sabellids, such as *Eudistylia polymorpha* and *Sabella media* which sometimes occur with *Pseudopotamilla ocellata*, have failed to reveal the presence of a single "Lar" on the tubes of these other worms. This may be due to the fact that these worms commonly grow to a considerably larger size than the common host and are for this reason an unsuitable substrate. Other sabellids, such as *Myxicola* and *Eudistylia vancouveri*, have tubes whose consistency or structure make it impossible for this hydroid to live upon them. Of the several different sabellids examined from Monterey Bay and vicinity only a single example of "Lar" upon any host other than *Pseudopotamilla ocellata* has been found, and this was a small colony on the tube of *Pseudopotamilla intermedia*. This worm had built its tube of elongate, rather pointed, sand grains and presented a much more irregular substrate to the hydroid than the tubes of its regular host. It appears that *Proboscidactyla circumsabella* is limited to hosts whose tubes do not reach very large sizes, whereas *P. flavicirrata* may be found upon tubes up to about 1 centimeter in diameter. The largest worm tube upon which *P. circumsabella* has been found was about 4 millimeters in diameter.

Proboscidactyla occidentalis (Fewkes)

In 1889, Fewkes described a medusa, *Willia occidentalis*, from near Santa Cruz Island. From his description it is clear that this medusa is a *Proboscidactyla*, and, moreover, it is presumed that this species is identical to that found at La Jolla, California, because a single specimen collected in 1950 near Santa Cruz Island is identical to the more abundant La Jolla material. Thirty-one medusae with 8–40 tentacles have been examined from the San Diego area, as well as a single 28-tentacle specimen from Santa Cruz Island plus 18 colonies of a hydroid which have been assigned to this species. The hydroids were found on sabellid tubes which were associated with a kelp holdfast. This kelp holdfast was growing in 40 to 50 feet of water and was obtained by Conrad Limbaugh on April 12, 1952, while diving with an aqua-lung at La Jolla. The samples from which the medusae were obtained were collected by Conrad Limbaugh, Robert Bieri, and John Bradshaw, of the Scripps Institution of Oceanography.

THE MEDUSA: Medusae of this species have been found in plankton samples collected at Santa Cruz Island in the month of March, 1949, and from La Jolla and San Diego Bay during the months of March through July, 1952. The largest medusa collected was a female 3.5 millimeters high by 3.5 millimeters in diameter. This medusa possessed 40 well-developed tentacles. The smallest medusa was slightly greater than 1 millimeter in height and diameter and possessed eight tentacles. In life little pigment is to be seen on these medusae, except for the dark reddish-brown to black bulbs of the tentacles. Some specimens show a little light-brown pigment in the stomach walls.

The gonads are apparent on 8-tentacled medusae but do not begin to bulge from the adradial walls of the stomach until about the 16-tentacle stage. The gonads appear ripe at the 32-tentacle stage, and the female possessing 40 tentacles seemed to have shed part of the eggs from one quadrant of the gonads. As in the other species of *Proboscidactyla*, the gonads do not fuse across the radial margins of the stomach and are disposed as four interradial masses consisting of paired adradial lobes connected at the interradii by thin sheets of gonadial tissue. The gonads, when fully ripe, show folds along their medial surfaces. The sexes are separate.

The manubrium is very short and the lips are highly folded. This species closely resembles *P. flavicirrata* in this respect.

The radial canals branch, and the general pattern and order of development is presented in Figure 1*a–c*. Small variations in the location and length of the branched canals occur from quadrant to quadrant and specimen to specimen; however, the order and final arrangement seems to be relatively definite so that when the 32-tentacle stage has been reached a difference in pattern of branching is apparent when it is compared with the same stage of *P. circumsabella*. This difference consists of a pair of fourth order tentacles spanning the second order tentacle in *P. occidentalis*, whereas in *P. circumsabella* a pair of fourth order tentacles span the left hand third order tentacles (compare Fig. 1*c* and 1*f*).

In the figure of this species in Fewkes (1889) a 20-tentacle medusa is shown. This is presumably a fleeting stage in development in which the first of the fourth order tentacles had appeared. The radial canals shown in Fewke's figure represent a condition seldom attained in this species in that he has shown the canal branched into three equal parts, with each of the lateral branches possessing another branch. The manner in which the canals of all species of *Proboscidactyla* branch is such that this is nearly an impossibility. It is presumed that Fewkes drew a symmetrical diagram which was not a copy of the actual pattern present. It will be noticed, if one compares the figures of the three species of this report showing the systems of branching canals, that *P. occidentalis* and *P. flavicirrata* tend to present a pattern in which the primary radial canal of each quadrant bifurcates rather symmetrically, whereas in *P. circumsabella* the primary canal seems to run directly to the margin, giving off its branches laterally. This difference is not absolute but applies in most specimens.

A ring canal was present in most of the individuals observed, although the specimens possessing 32 or more tentacles did not show this structure. The disappearance of the ring canal seems to be a characteristic of adulthood of this genus.

The bell of this species is somewhat thicker then that of the other two species, and, also, the tencency for the height to be the same as, or greater than, the diameter is striking. In preserved specimens the adoral end of the stomach never is located more than half the distance from the velar opening to the adoral tip of the bell (see Fig. 7). Fewkes (1889) described a slight constriction in the external outline of the bell at a level with the base of the stomach and showed this constriction in his figure. This constriction was apparent in two of the 31 specimens examined but apparently is not characteristic of the species.

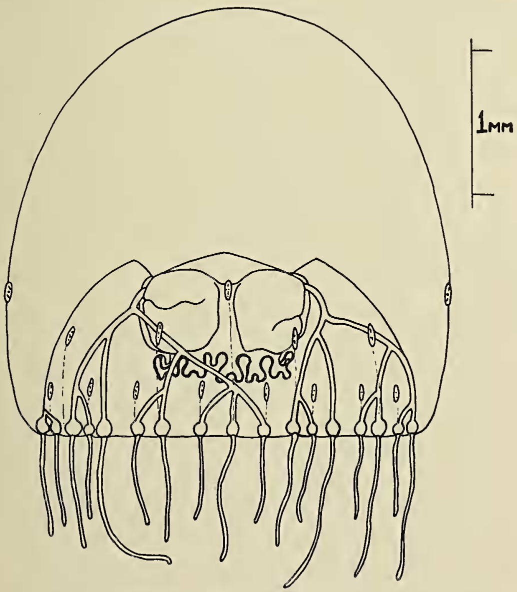

FIG. 7. *Proboscidactyla occidentalis*. Whole medusa with tentacles shown on one half only.

More commonly the bell is hemispherical or is of an elongate shape such as could be depicted by a figure representing slightly more than half of an oval.

The nematocysts of the medusa present a familiar pattern. Only two kinds, macrobasic euryteles and desmonemes, are present, but a rather unusually shaped medium-size macrobasic eurytele occurs in the cnidothylacies. This nematocyst (Fig. 3*h*) is distinctive of this species. In the tentacles a more usual, small, macrobasic eurytele is numerous, as are desmonemes. The nematocysts of this species were found to be as follows:

Cnidothylacies	
Large macrobasic euryteles	$24-28 \times 11-14\mu$
Medium macrobasic euryteles	$12-17 \times 8-12\mu$
Desmonemes	$5-6 \times 4-5\mu$
Tentacles	
Small macrobasic euryteles	$7-10 \times 4-5\mu$
Desmonemes	$5-6 \times 4-5\mu$

Figure 3*g–j* illustrates the nematocysts of this species.

THE HYDROID: The hydroid stage of this species resembles in its general form that of other known species, its most singular character being that the gonophores bear large numbers of medusa buds which were not discerned to have a regular arrangement upon the gonophores. A maximum of 12 buds was found to occur on a single gonophore among the colonies examined. This material was collected on April 12, 1952.

The gastrozooids are arranged around the lips of sabellid tubes, sometimes forming a complete circle, the two tentacles and mouth facing the orifice of the tube. One colony, which was growing on a tube which was damaged on one edge, was located about 1.5 millimeters inside the lip of the tube. Because of the manner in which the lip of the damaged tube flared out, this placed the colony in direct contact with the bases of the worm's tentacles, which is the normal position, although its location inside the tube was unusual. The hydrorhizal net of this specimen started on the outside of the tube, traveled up the tube to its lip, and then down inside the tube to the ring of gastrozooids. The location of this colony suggests that the individuals may have migrated from the old lip to the new position, although it may be that the hydroid settled upon the tube after it had been damaged. It is not known how "Lar" responds as its host lengthens and enlarges its tube, if indeed the worm does so, after a colony has established itself upon it.

The individual gastrozooids are never more than 1 millimeter tall and are rather stout, being 0.2 to 0.3 millimeter thick. The nematocyst pad on the "head" is well developed and is devoid of pigment, as is the ectoderm in general. The endoderm is brown.

The gastrozooids are connected to one another via a network of anastomosing, naked hydrorhizae, these hydrorhizae not exceeding 0.1 millimeter in diameter.

Tentacleless gonozooids occur as scattered individuals arising from the hydrorhizal net. The gonozooids are about 1 millimeter tall and bear a capitate, mouthless tip which is studded with nematocysts. From 2 to 12 medusa buds are borne on each gonozooid. They arise at irregular intervals slightly above the mid-point. The medusa buds show four spots of brownish-red pigment which correspond to the developing first order tentacle bulbs and also a brownish pigment mass representing the developing stomach. Medusa buds were seen pulsating on several colonies, but none were released before the specimens were preserved.

The nematocysts of the hydroid were studied and found to be as follows:

Macrobasic euryteles	20—28×8—11μ
Large microbasic euryteles	12—24×4— 6μ
Small microbasic euryteles	5— 8×2— 3μ
Desmonemes	6— 9×3— 4μ

The tentacles seem to possess only the small microbasic euryteles, whereas the macrobasic euryteles and desmonemes occur only in the cap of the gastrozooid. The large microbasic euryteles occur on the body of the polyp as well as in the cap. The body of the polyp also has small microbasic euryteles. Figure 5*i–l* illustrates the above nematocysts.

THE HOSTS: This species (*P. occidentalis*) has been found on two species of sabellids, *Potamilla neglecta* and *Pseudopotamilla intermedia*. These worms were kindly identified by Dr. Olga Hartman of the Allan Hancock Foundation. Sabellids are not well represented in the intertidal region near La Jolla, and only a few small specimens of *Pseudopotamilla intermedia* have been collected. These did not have any "Lar" upon them. The material upon which the hydroid was found was taken from 40 to 50 feet of water, as mentioned earlier.

DISCUSSION

A group of organisms, such as is represented by the genus *Proboscidactyla*, presents a number of interesting problems to the biologist. One of these problems concerns the matter of symbiosis, more specifically commensalism in this instance, and a second concerns the special life history of this group with the unavoidable complications encountered where the two phases of the life history are adapted to, or are adapting to, very different environmental factors.

In the Hydrozoa the tentacles, with their associated nematocysts, represent the primary tools for protection and food gathering, and there are few hydrozoans which can be pointed to as possessing reduced numbers of tentacles. *Protohydra* and *Tetraplatia* are curious among the Hydrozoa, indeed among the Coelenterata, in that these free living animals possess no tentacles at all. On the other hand, among the symbiotic Hydrozoa a rather large group of hydroids exists which possesses reduced numbers of tentacles, and some have none. Such forms as *Hydrichthys*, *Icthyocodium*, and *Nudiclava* are tentacleless, whereas *Monobrachium* has but one and *Proboscidactyla* but two tentacles. The possibility exists that the tentacleless forms exhibit a true parasitism in which the hydroid uses the hosts' tissues for its food, as was claimed for *Hydrichthys* by Warren (1916). The exact manner in which *Monobrachium* is adapted to its bivalved host is not clear inasmuch as living specimens have not been studied, but for at least two of the 2-tentacle *Proboscidactyla* we have adequate descriptions of tle living animal (Gosse, 1857; Hand and Hendrickson, 1950). From these descriptions we can see how well fitted these animals are for their special way of life, but they seem to have sacrificed certain usual hydroid traits and the versatility of substrate requirements of most hydroids for the limited substrate offered by certain sabellids. The known genera upon which these hydroids occur represent but a small number of those which appear to be available. Only *Potamilla*, *Pseudopotamilla*, and *Schizobranchia* have so far been reported as bearing *Proboscidactyla*. Studies concerning host choice and relationships among this group would appear to be worth pursuing.

In most respects the life history of *Proboscidactyla* differs but little from that presented in freshman biology as characteristic of the Hydrozoa. However, a life history such as this, with two well-developed, relatively long-lived phases, is rather unusual in the animal kingdom and presents certain difficulties to the student of the group. The hydroid phase is, in general, a sessile stage, adapted to its own environment, whereas the medusoid stage is pelagic and is adapted to a completely different mode of life. Most students of the Hydrozoa look upon the hydroid phase as a stage in development specialized for asexual propagation and upon the medusa as the adult, sexually reproducing stage of the life history. Because of this curious division of the life history, students of the Hydrozoa have developed two "schools," the one a group of specialists in hydroids, the other in hydromedusae. Therefore, we find today that in many instances there are two sets of nomenclature referrable to a given animal, and there is no immediate hope of reducing this gigantic taxonomic snarl to a satisfactory systematic treatment. The prime hope would seem to be the study of life histories in this group so that the medusae may be referred to their proper hydroids, and then gradually the two systems will become one.

In the nearly 100 years since Gosse (1857) described the first "Lar," only three additional species have been described. These three all occur along the Pacific coast of North America, with one of them ranging to Japan. The actual number of species which exist cannot be determined at this time, but the possibility that as many as a dozen occur is not improbable. Uchida and Okuda (1941) list four certain species of medusae of *Proboscidactyla* with a fifth, originally described by Uchida (1927) as *Misakia typica*, also included as a distinct species. The status of several of the ten species and varieties of *Proboscidactyla* and *Willia* of Mayer (1910) certainly remains in doubt, although the present study validates Fewkes' *Willia occidentalis* and adds a new species, *Proboscidactyla circumsabella*. Foerster (1923), in an excellent study of the hydromedusae of the west coast of North America and particularly of the Vancouver Island region, lists four species of *Proboscidactyla*. Of these, two are merely cited from the literature (*P. occidentalis* and *P. ornata* var. *stolonifera*), but the other two (*P. flavicirrata* and *P. polynema*) concern specimens taken in the Vancouver Island area. Foerster reported ocelli on the tentacle bulbs of *P. flavicirrata;* however, this statement and that of Uchida and Okuda (1941) are the only known instances where ocelli have been reported for proboscidactylans. In each instance, however, the report has concerned *P. flavicirrata*, so ocelli may occur in that species although specimens examined by the writer have not possessed ocelli. The species *Proboscidactyla polynema* of Foerster is referred to the animal described from the Atlantic by Hartlaub (1917) as *Pochella polynema*. This medusa has no cnidothylacies (centripetal canals of Foerster), and each primary radial canal gave off about six lateral branches on each side. These characters would make this an unusual species of *Proboscidactyla*, if, indeed, it is one at all.

The following four species of *Proboscidactyla* now have been described for both the hydroid and medusoid stage of the life history.

P. stellata (Forbes) (Hydroid *Lar sabellarum* Gosse)
P. flavicirrata Brandt
P. occidentalis (Fewkes)
P. circumsabella n. sp.

This leaves an ample number of hydroid stages to be described, such as the several which presumably live along the Atlantic coast of the United States. At least one of these hydroids is known to occur in Long Island Sound (E. S. Deevey, *in litt.*). This hydroid will probably be identified with the medusa *P. ornata* (McCrady) when a critical study is made.

In considering a group of species it is always interesting to see if a key to their evolution or the manner in which they are related can be found. A group such as *Proboscidactyla* has no fossil record to help us, and today they are widely distributed. At least four species occur in the Pacific and an equal number in the Atlantic. This does not immediately suggest a key to their evolution.

If the hydroid stages of *Proboscidactyla* are compared, certain relationships are suggested. *P. stellata* and *P. flavicirrata* both have gonophores borne close to or upon the gastrozooids, whereas neither of the other two species whose hydroids are known is so constructed. Also, *P. stellata* commonly produces six-rayed medusae, whereas *P. flavicirrata* may have four, five, six, or eight radial canals. This suggests a relationship between these two, as the other two species seldom if ever produce anything other than four-rayed medusae. The nematocysts of the polyp stages of *P. stellata* and *P. flavicirrata* also resemble each other very much, but they also closely resemble those of *P. circumsabella* and *P. occidentalis*.

The gonozooids of the four species do not give us much help beyond their location on the colony. In *P. stellata* four medusa buds are usually produced, whereas *P. flavicirrata* may have up to eight buds; *P. circumsabella* seems never to produce more than four, whereas *P. occidentalis* produces up to 12.

The adult medusae of *Proboscidactyla* seem to offer the best evidence to their paths of evolution. *P. stellata* and *P. flavicirrata* have already been mentioned as having six or a variable number of radial canals, respectively, and it should be mentioned that *P. mutabilis* of the South Atlantic is even more variable than these two species. Of the three species of the present report, the northern species (*P. flavicirrata*) is largest and has more tentacles than its two southern relatives.

The nematocysts of the medusae are known for only the three species reported herein. Of the three, *P. occidentalis* is the most distinctive in that three sizes of macrobasic euryteles are present of which one, the medium size, is very unusual in shape. *P. flavicirrata* and *P. circumsabella*, on the other hand, possess only two sizes of macrobasic euryteles. If the nematocysts of the medusae are used to indicate relationships, it appears that the latter two species are more closely related to each other than to *P. occidentalis*. In summary, then, it appears that *P. stellata* and *P. flavicirrata* are closely related, the latter being also near *P. circumsabella*. *P. occidentalis* is somewhat more distantly related to these others in both its morphology and its geographic location.

Another interesting medusa, *P. ornata* (McCrady) var. *stolonifera* Maas, has been reported from the Pacific at Acapulco harbor (Mexico) by Bigelow (1909) and from the Malay Archipelago by Maas (1905). This variety should be elevated to at least the rank of subspecies and will be so considered in this study. *P. ornata stolonifera* is a good-size medusa (about 5 mm. diameter) but has few tentacles as compared to other Pacific species, its maximum number being about 20. Also, it is distinctive from other Pacific species in its possession of medusa-bearing stolons. It appears that this subspecies has been derived from the Atlantic *P. ornata–P. ornata gemmifera* complex, *P. ornata* (McCrady) being known from southern New England to Beaufort, North Carolina, and *P. ornata* (McCrady) var. *gemmifera* Fewkes (see Mayer, 1910, for first usage of this combination) from North Carolina to the Bahamas. As in the instance of the variety *stolonifera*, this variety (*gemmifera*), will be considered a subspecies. The species *P. ornata* is distinguished from its subspecies, *P. ornata gemmifera*, by the habit of the latter of producing medusa-bearing stolons which arise from the radial corners of the stomach. Thus we have an interesting series of medusae, ranging from New England to the Bahamas, which, as southerly regions are reached, seem to develop the character of asexually producing medusae from the medusa stage, and this southern form has a close relative in the warm waters of the Pacific which has a similar characteristic. If one allows the speculation, it seems possible that the Pacific *P. ornata stolonifera* was separated from the Atlantic *P. ornata gemmifera* after a period of submergence and emergence of the Panamanian Isthmus. It would be of real interest to study the host substrates of the "*ornata* complex" to see if these worms are related in a manner similar to that of the medusae.

Kramp (1952) has reported *Proboscidactyla ornata* from the west coast of Chile. He had but a single 3-millimeter specimen at his disposal, and this specimen was not in good shape. The possibility that *P. ornata* exists along the coast of Chile will not be denied; however, it may well be that this particular specimen really represents a young specimen of *P. mutabilis* or an undescribed species. That Kramp's medusa was not a *P. ornata* seems even more likely if one considers the known distribution of this species and its subspecies in conjunction with the existing current systems (see, for example, Chart VII in Sverdrup, Johnson, and Fleming, 1946).

Uchida (1927) rather thoroughly surveyed the anthomedusan fauna of Japan and in this study listed five forms of what now make up part of the genus *Proboscidactyla*, but did not at that time recognize *P. flavicirrata* as occurring in that area. In a subsequent report Uchida and Okuda (1941) reported from Japan a hydroid and medusa they took to be that of *P. flavicirrata*, which I assume to be correct. The identification of *P. ornata* and *P. ornata gemmifera* in Japan (Uchida, 1927) presents a problem in distribution and systematics. The *P. ornata* may well be the young of *P. flavicirrata*, but the phenomenon of budding in the medusoid stage has not been reported for this latter species, so that there is no ready suggestion as to what this budding form may have been. That *P. ornata* and some of its subspecies do or do not occur in Japan cannot be stated with certainty at this time. Moreover, the answer to this riddle may lie in the fact that the ability of medusae of this group to reproduce asexually may be more widespread than is now realized. A number of possibilities as to the identity of Uchida's *P. ornata* and *P. ornata gemmifera* certainly exist. The species *Willia stellata*, *Willia pacifica*, and *Misakia typica* of Uchida (1927) would best seem to be considered as synonyms of *P. flavicirrata*, although the critical test of this statement must await a study of their nematocysts.

In the many records of the occurrence of *Proboscidactyla*, one notable fact is that these medusae are absent from the high seas. They occur instead in bays and along the coasts of most parts of the world. This distribution must certainly be the result of the dependence of the hydroid upon sabellids, which worms are most common in shallow water. A second curious phenomenon concerning the distribution of *Proboscidactyla* is the extremely wide range of the species, *P. ornata*. Kramp (1952) lists this species from the Pacific coast of Mexico, Japan, the tropical Pacific, the Malayan Archipelago, and from Madras, India, and, further, from the Atlantic coast of North America, the Bahamas, Brazil, and Fernando Po on the west coast of Africa. The other species have much more localized distributions. Maas (1905) has pointed out that the habit of budding practically puts *Proboscidactyla* in a class with holoplanktonic organisms. Actually, the habit of budding does not seem to be a character of the genus but rather of the subspecies of *P. ornata* which, indeed, may well account for its curious and widespread distribution.

At this time it would appear that the following species exist, occupying in general the following areas. Most of the literature relevant to these distributions has already been cited, and that which has been omitted can be found in Mayer (1910) or Browne and Kramp (1939).

1. *P. flavicirrata*	North Pacific
2. *P. circumsabella*	Central Californian Pacific
3. *P. occidentalis*	Southern Californian Pacific
4. *P. stellata*	European North Atlantic
5. *P. ornata ornata*	Atlantic, New England to North Carolina
6. *P. ornata gemmifera*	East and West Tropical Atlantic
7. *P. ornata stolonifera*	East and West Tropical Pacific to Indian Ocean
8. *P. mutabilis*	South Atlantic and Straits of Magellan

The above species may be related and may have evolved along the following lines, but, of course, this is speculative. To begin with, I suggest a northern, inherently variable medusa such as *P. flavicirrata* which possibly as a circumpolar species gave rise to the Atlantic *P. stellata*. *P. flavicirrata* or its predecessor also gave rise to *P. circumsabella* and to *P. ornata*. *P. ornata* seems to have developed its southern subspecies *gemmifera* in the Atlantic which by spanning the Panamanian Isthmus has given rise to the subspecies *stolonifera* which has spread via the tropical current systems throughout the tropical Pacific. *P. occidentalis* may be the offshoot of *P. ornata stolonifera* or of *P. circumsabella* or some other species. The origin of *P. mutabilis* of the Falkland Islands and perhaps of the Pacific is not apparent. However, another pattern of evolution can be suggested which, based upon major existing ocean currents, seems even more plausible. Thus, starting with the variable *P. mutabilis* and utilizing the currents of the South Atlantic Ocean, medusae could be carried to the Isthmus of Panama, to the Gulf Stream, and into the North Atlantic to England. The Pacific species could be derived from a crossing at Panama or by moving directly into the Pacific from the circumpolar Antarctic currents. It would be possible to start at almost any point in the oceans and arrive at the same end results.

It is, of course, not necessary to accept any point or species as the origin of this group of medusae; the important fact would seem to be that today *Proboscidactyla* is a genus which occurs in most oceans and presumably has spread to these oceans via ocean currents acting upon the planktonic medusoid phase of its life history. One factor which would appear to limit the distribution of this genus in its spread would be a lack of suitable hosts. Therefore, if this group and its evolution are to be understood adequately, further studies are needed not only on the hydroids and medusae but also on the sabellids to whose fate *Proboscidactyla* has apparently attached its own hopes for the future.

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